

REPRODUCTIVE BEHAVIOR OF
CLAEODERES BIVITTATA
(COLEOPTERA: BRENTIDAE)*

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Promiscuous aggregations of adult brentid weevils often occur on host trees, where females gather to oviposit (Meads 1976; Johnson 1982). In such a circumstance, in which a male can potentially inseminate many females, intense competition by males for females typically occurs (cf. Thornhill 1976; Alexander and Borgia 1979; Fincke 1982). In addition, members of the family Brentidae show considerable intraspecific variation in adult size (Sharp 1895; Soares 1970; Damoiseau 1967). From the numerous studies that show that larger body size enhances competitive aggressive success (e.g. Johnson and Hubbell 1974; Hamilton et al. 1976; Heinrich and Bartholomew 1979), it might be predicted that larger male brentids would enjoy greater mating success in breeding aggregations, and—provided that male size is an important competitive characteristic—that variation in male mating success would be commensurate with variation in male body size. I tested these predictions on an aggregation of *Claeoderes bivittata* Kirsch. (Coleoptera: Brentidae) in which the adults varied more than ten-fold in body weight.

The results of the present study support the idea that body size is an important trait. Males of nearly equal size engaged in a ritualized contest which appeared to permit sensitive assessment of relative size, and larger males enjoyed greater success in fights over females. However, small (11–22 mm) as well as large males (31–39 mm long) were disproportionately represented in mating. Small males had greater than expected success partly because they at times took shelter under, rather than guarded, their females, emerging for copulation when a larger rival was not present.

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MATERIALS AND METHODS

Claeoderes bivittata adults were studied on a dying tree of *Quararibea asterolepis* (Bombacaceae) on Barro Colorado Island (9°09' N, 79°51' W) in the wet season of 1980.

On June 9 all weevils from ground level to 2 m on the standing tree were collected, placed in a bag, sexed, measured in length to the nearest mm, and replaced. On June 13 all weevils up to a height of 2 m were collected and brought to the laboratory, where they were sexed, measured, cleaned of most mites with masking tape, and weighed to the nearest tenth mg on a Mettler H35AR balance. On June 14 these weevils were replaced on the trunk. On six dates between June 28 and July 14 the behavior of individually marked weevils of different sizes was described into a portable tape recorder, for a total of 13 hours. Rectangular and trapezoidal arenas about 1/3 m² were drawn on the sides of the trunk between buttresses. On a given date the trunk was circled clockwise. The reproductive and competitive behavior that was centered around all male-female pairs in an arena was recorded, until none of the pairs originally in the arena remained. Durations of acts were timed with a stopwatch. Weevil density on the trunk slowly dwindled from 27–36/m² on June 28 to 15 or fewer/m² on July 14. A few weevils were collected in alcohol for identification and dissection.

DESCRIPTION OF WEEVIL ACTIVITIES

Oviposition

Before drilling, a female walks slowly over the smooth trunk, touching the substrate with her antennae. When a favorable site is found the female chews for 30–60 min until her rostrum is buried to the depth of the antennal insertion. Periodically she withdraws her snout, lifts her head, and expels sawdust from her jaws.

To oviposit, a female turns around and locates the drilled hole by tapping with rear end and hind legs. She then everts her telescoped sclerites, bringing the ovipositor to the hole, and remains still for 70 sec to 3 min. The hole drilled is the right size for one egg.

After oviposition the female rocks by bending and straightening her forelegs 12 times per min for 3.5–12 min, repeatedly moving the tip of her abdomen between the hole and positions further back. As the female rocks out, a bristled tergite is everted, to which bits of

sawdust and other debris adhere. As she rocks in, the material appears to be added to the hole.

A female may drill and oviposit three times in succession (Fig. 1).

Female Aggression

Aggression is instigated by females before they drill and by females that have just completed oviposition. The aggression is usually directed against drilling females. The encounter may involve only an intention movement, or the instigator may push, poke, or swat a drilling female with her snout, or pry her out of her hole by sticking the snout under her abdomen and lifting. A fleeing female may be pursued several cm. Reciprocated aggression may result in a fight lasting 6 min or more in which the combatants kick, face one another and swivel their heads and forebodies, or thrust the snout under the other and lift suddenly; females of the same length may also stack themselves head-to-tail and sweep their snouts over the tip of their opponent's abdomen. Fights end when a female leaves or is flipped from the tree.

Guarding

A guarding male stays with a female as she antennates the trunk, drills, or oviposits, keeping his rostrum or his body over her (Fig. 2). He responds aggressively if a rival male draws near, and he may also threaten a female if she approaches his female too closely, by facing her, advancing on her, or chasing her with a yawing movement of the head.

Mating

A male mates with the female he is guarding one to several times during drilling, and is especially likely to do so just before the female pulls her beak out of the wood to oviposit (the onset of oviposition occurs less than a minute after the termination of copulation in about 80% of the cases (see Fig. 1)). A few seconds before mating a male accelerates his movements, antennates the female, and then mounts, sometimes trying the female's head. Copulation lasts about a minute.

Rejection

A female not ready to drill or oviposit will walk away from males that approach. A drilling female can thwart mating attempts by walking her hind end in a circle around the pivot point of her snout in wood, or by withdrawing her snout entirely and walking away.

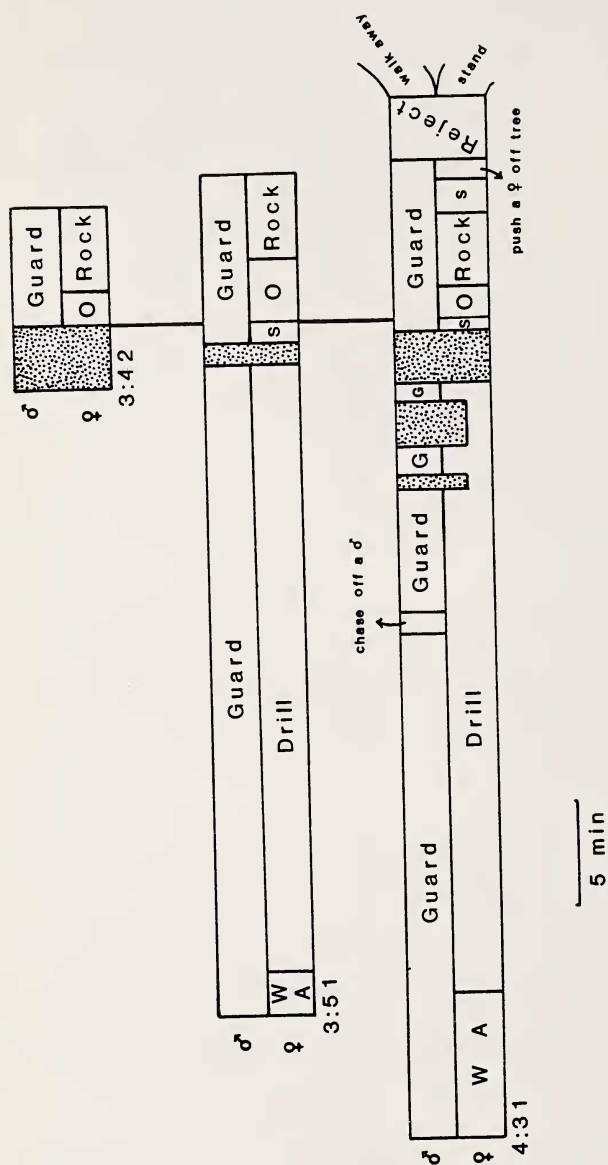


Fig. 1. Behavior of 33 mm male and 25 mm female in period spanning three successive ovipositions, from 3:42, when first seen together, until 5:22, when they parted company. Duration of activity is indicated to nearest half-minute. Above midline, male activity. Below midline, female activity. Stippled blocks = copulation. G = guard, O = oviposit, WA = walk and antennate trunk, S = stand. The onsets of oviposition are aligned over one another; notice that oviposition is immediately preceded by copulation.

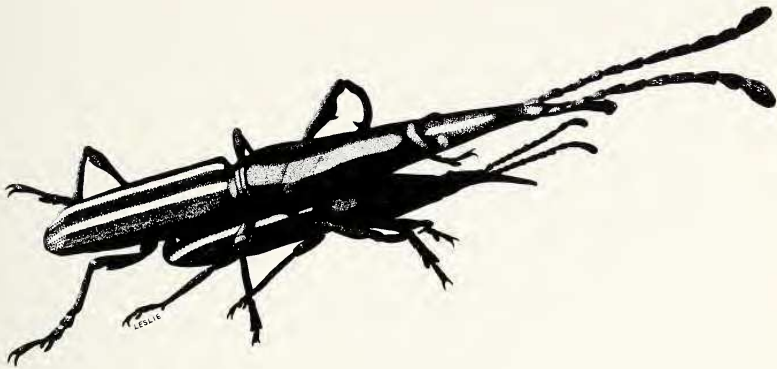


Fig. 2. A male, with enlarged jaws for nipping rivals, guards a female *Claeoderes bivittata* as she prepares to drill an oviposition hole. A guarding male typically places all or part of his body (particularly the rostrum) over the female. A small male in the presence of a large male, however, may insert himself partly under the drilling female.

Male Aggression

Males fight for access to females. Initially they may intermingle, jerk, or lash their antennae. Attacks involve nipping, kicking, poking with the snout, or putting the snout under the rival's body and jerking upwards 3 times/sec. A male may also interfere with copulation by thrusting his snout between a mating pair and pushing. An attacked male may flee, or reciprocate in kind.

Two males of approximately the same length may engage in a more stylized contest in which they align themselves, side by side, 1–10 mm apart, facing opposite directions. On the side of the rival a male taps his antenna and hind leg 4–5 times/sec, and when the opponent does likewise, the males fence leg against antenna at either end. The "appendage-fencing" contests observed in this study lasted 3 sec to 9 min.

RESULTS

Size Variation

Male weevils in the June 13 sample ($n = 67$) ranged from 12–38 mm in length and from 19–334 mg wet weight, i.e., the biggest male was 3 times as long and 17 times as heavy as the smallest. Males 11

and 39 mm long were found subsequently. The females ($n = 81$) ranged from 12–29 mm and 19–247 mg with the biggest female $2\frac{1}{2}$ times as long and 13 times as heavy as the smallest. At all lengths females were heavier than males, and they increased in weight faster with length than did the males (Fig. 3).

A frequency histogram of the lengths of males ($n = 101$) and females ($n = 128$) measured June 9 is shown in Fig. 4. Mean male length \pm S.D. was 25.91 ± 7.21 ; mean female length \pm S.D. was 20.97 ± 4.35 .

Five females were dissected. Each had two ovarioles and 3 or 4 large, yolked eggs. The length of the largest yolked egg increased monotonically with female length, from a 1.3 mm egg in a 13 mm female to a 2.1 mm egg in a 29 mm female.

Size and Aggressive Success

In aggressive encounters between females the female that fled was deemed the loser. The winners by this criterion were larger in 14 of 14 contests involving weevils of unequal length ($p = .0001$, sign test). Even if four additional encounters involving females of equal length were conservatively counted as victories for the smaller weevil, the winners were still significantly more likely to be the larger ($p = .0154$).

In male encounters the winner was considered to be the male that remained by the female. Here again the larger weevil was significantly more likely to win ($p < .005$, sign test). Defending males (the ones originally with the female) were not significantly more likely to win encounters than intruding males ($p \approx .18$).

The relative size of the rivals was also a factor in the occurrence of the appendage-fencing contest. An analysis of the differences in length between the rivals in five encounters in which the contest occurred and sixteen encounters in which it did not, showed that rivals using the contest were significantly more similar in length ($p = .002$, Mann-Whitney U test). The mean \pm S.D. difference in length for rivals using the contest was 1.8 ± 2.0 mm; for rivals not using it, 8.1 ± 7.4 mm.

One effect an intruding male may have, whether or not he wins the female, is to shorten the duration of the defending male's copulation. Uninterrupted copulations lasted a mean \pm S.D. of 82.4 ± 48.7 sec, with $2/3$ of the copulations lasting between 40 and 90 sec. Copulations interrupted by rivals, however, lasted 31.0 ± 15.1 sec ($p = .026$, Mann-Whitney U test).

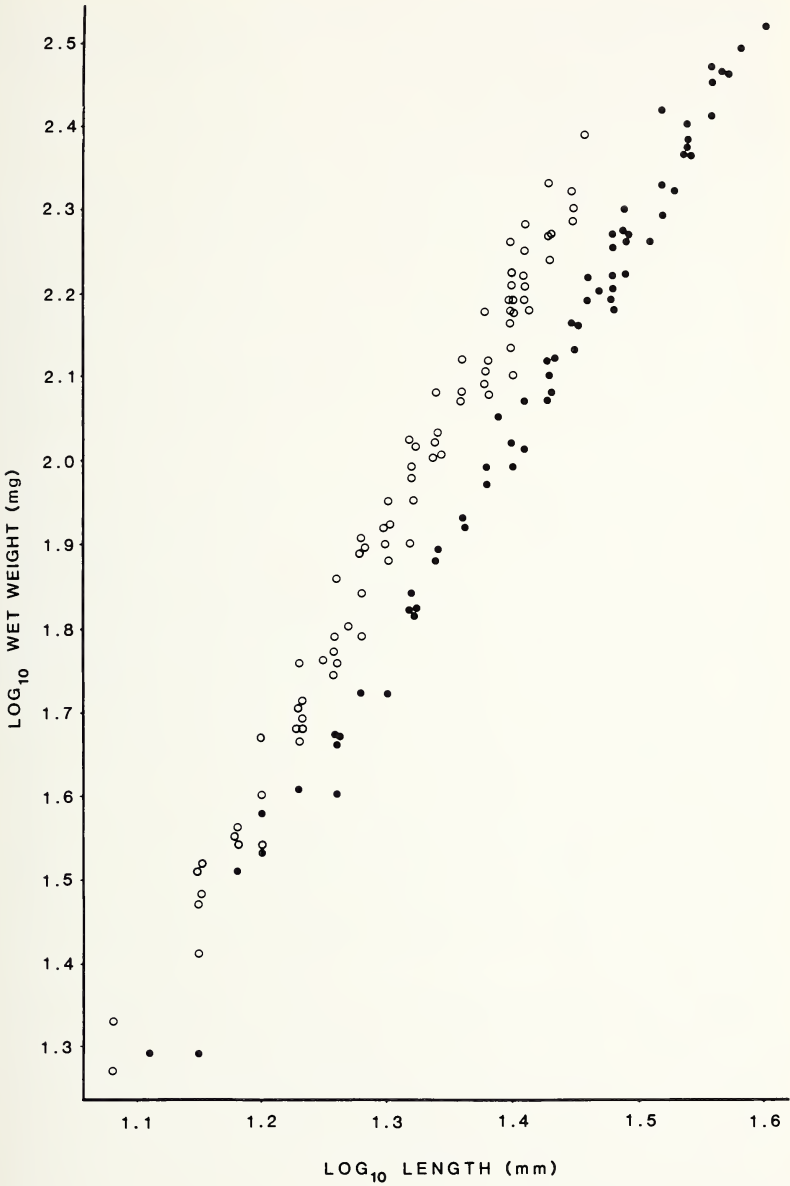


Fig. 3. \log_{10} length (mm) vs. \log_{10} wet weight (mg) of male (●) and female (○) *Claeoderes bivittata*. For males, $\log_{10}(\text{weight, mg}) = -1.53 + 2.54 \log_{10}(\text{length, mm})$. For females, $\log_{10}(\text{weight, mg}) = -1.78 + 2.83 \log_{10}(\text{length, mm})$.

Size and Mating

Individual weevils were compatible with mating partners of many sizes. In 52 different pairings, females mated with males as much as 10 mm shorter than themselves, and males with females as much as 16 mm shorter. Despite this, mating was size-assortative overall. The Pearson product moment correlation for male and female length was $r = .323$ ($p = .021$) for the 52 different pairings, and $r = .398$ ($p = .002$) if multiple matings of a pair were included.

Females, however, tended to reject males smaller than themselves when such males attempted to mate. In 57% of the cases of rejection (4 out of 7) the female was larger, whereas in only 37% of the cases of mating (22 out of 60), was the female larger. When lengths of males rejected and accepted for mating were examined, it was found that rejected males were shorter ($p < .05$, 1-tailed, Mann-Whitney U test).

Given the more frequent rejection of small males, and the greater success of larger males in aggressive encounters over females, it was expected that males found mating would tend to be larger than males simply present in the aggregation. Whereas females that mated were larger than unattended drilling females ($p < .02$, 2-tailed, Mann-Whitney U test), males that mated were not significantly larger than guarding males, males in a random sample, or males that were alone (Table 1). Instead, a frequency histogram of mating males showed a bimodality in the size of males that mated compared to an unimodal distribution of males in the breeding aggregation (Fig. 4). There appeared to be a dearth of medium-sized mating males. Indeed, a chi-square test on the 52 different pairings found that mating males were significantly more likely to be large (≥ 31 mm) or small (≤ 22 mm) than would be expected if they mated in proportion to their abundance in the random sample ($\chi^2 = 4.87$, 1 df, $p = .027$).

Extra opportunities for small males to mate could arise if guarding males drove away small rivals less frequently than they did rivals more their size. With this in mind, I compared the 7 cases in which two males co-occurred at a drilling female for 3 min or more with the 19 cases in which one male drove off the other within the first minute. In 6 of the 7 cases of co-occurrence, one male was small (≤ 22 mm) and the other large (≥ 31 mm). In the remaining case both males were medium-sized. In the 7 cases of co-occurrence the

Table 1. Lengths (mm) of *Claeoderes bivittata* individuals in different categories. The two means marked with an asterisk are the only two compared within a sex that are significantly different.

Females				Males			
	n	\bar{x}	S.D.		n	\bar{x}	S.D.
♀♀ drilling alone	11	19.73*	2.45	♂♂ without partners	14	25.21	7.30
Guarded, drilling ♀♀	49	20.08	3.67	Guarding ♂♂	49	24.55	6.76
Random sample of ♀♀	128	20.97	4.35	Random sample of ♂♂	101	25.91	7.21
♀♀ that mated	52	22.21*	4.20	♂♂ that mated	52	24.77	8.09

mean \pm S.D. size difference between the males was 13.6 ± 8.5 mm. In the 19 cases of intolerance, the mean S.D. size difference was only 5.8 ± 5.7 mm. The males in the cases of co-occurrence were, in fact, significantly more disparate in size ($p < .02$, 2-tailed, Mann-Whitney U test).

The joint attendance of a drilling female by the two medium-sized males was short-lived (4 min). The small and large male combinations, on the other hand, were more persistent ($\bar{x} = 19.8 \pm 10.5$ min). Stability was achieved in part because the small male kept a "low profile." The small males were unaggressive, even if poked, and 5/6 of them spent most of their time partway under the drilling female. Usually it was the rostrum that was tucked under the female, but two individuals crawled under the female at right angles to her long axis and centered themselves beneath her. Postures in which a male placed part of himself under the female were exhibited only by small males in the presence of a large male guard.

Opportunities to mate did arise for 5 of the 6 small males, despite the existence of the larger guards. Three of the small males mated while the large male was fighting off a large intruder. One small male mated while the large male stood with his snout resting on the female's head. Another small male waited until the onset of oviposition, when the large male left. He then interrupted the post-oviposition rocking behavior of the female in order to copulate. The small male that did not mate was driven off by the large male guard, who was aroused from quiescence by a 38 mm intruder who nipped him and mated with his female.

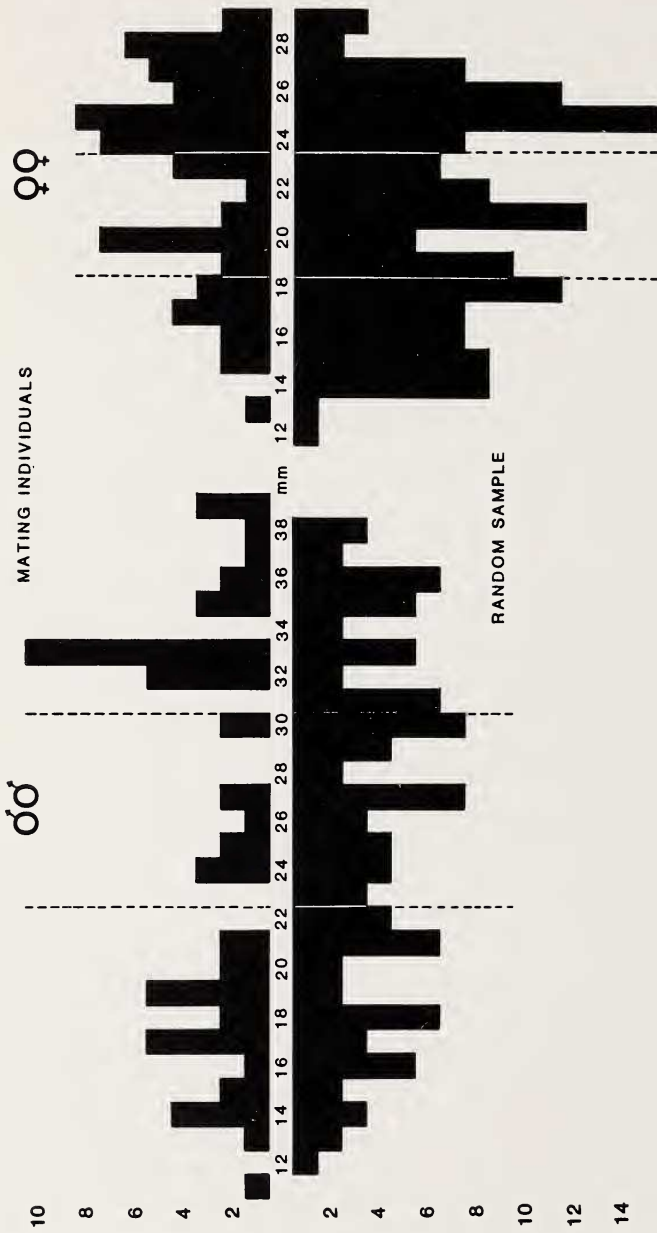


Fig. 4. Frequency of males (left) and females (right) in different length classes. Above the line: frequency distribution of mating individuals. Below the line: frequency distribution of individuals in the June 9 sample of the population. The dashed lines divide the June 9 sample into "small", "medium", and "large" weevil classes. Boundaries of these categories were arbitrarily established so that 31-36% (i.e., 1/3) of the weevils of one sex fell into each class.

Despite their mating successes, the small males were not the equal of the large ones. The copulations of the small males appeared to require the absence or inattention of the larger attendant. In contrast, the large males mated when they chose. All 6 large males, for instance, were the last to mate before the female oviposited, after which they left.

DISCUSSION

In *Claeoderes bivittata*, there is a great deal of variation in adult size, presumably due in part to variable growth conditions experienced by the larvae (Kleine 1933; Haedo Rossi 1961; Galford 1974; Peters and Barbosa 1977). As with another brentid, *Brentus anchorago* (Johnson 1982), the larger individuals have several reproductive advantages. In both species, larger females can clear from the region in which they just oviposited, more of their drilling rivals (thus possibly reducing later crowding of their larvae), and are less likely to be ousted from their chosen drilling site. Larger females also lay larger eggs, an initial advantage which in other beetles has been shown to significantly affect final adult size (Palmer 1983). Larger males do more mating than average, and assortatively mate with larger females who have the reproductive advantage of larger eggs and greater competitive success at oviposition sites.

There is, however, a principal difference between *B. anchorago* and *C. bivittata*. In *B. anchorago*, the bigger the male, the more he mates (Johnson 1982). In *C. bivittata*, the middle-sized males mate the least. In *B. anchorago*, males are highly intolerant of other males at a drilling female. In *C. bivittata*, a female can sometimes have two attendants if one is large and one is small.

The circumstances that permit the co-occurrence of a large and small male at one female need further investigation. In a proximal sense, small males may be less easily perceived than larger ones. Certainly, the small males appeared to assist this process by making themselves less conspicuous. They frequently tucked their snout under the female, along with the antennae which in other encounters permit male-male recognition. The small males were not seen to advertise their presence by initiating acts of aggression. Similar unprovocative tactics were noted in the smallest males of the wood-boring weevil, *Rhinostomus barbirostris*, at females guarded by large males (Eberhard 1980). Then too in the ultimate sense, it may

not be worth the energy expenditure for a large male to keep small, persistent males from the vicinity of the female. Despite matings by small males, large males may enjoy most of the paternity.

A true answer to the question of the relative reproductive success of large and small males awaits determination of the mode of sperm competition in *C. bivittata*. Whatever the mode, the relative reproductive success of a small male is probably less than the relative number of matings he achieves. If there is sperm mixing, the small males (which in the six cases observed here averaged 200 mg lighter than the males with which they co-occurred), probably transfer less sperm per copulation than the large ones. In two species of heliconiine butterflies, for example, smaller males transfer smaller spermatophores (Boggs 1981). If there is sperm precedence, we would expect large males, with the advantage of weight and strength in aggressive encounters, to copulate at will when the probability of fertilizing the egg is the highest. Small males, mating when they could, might or might not transfer sperm at the opportune time.

The mode of sperm competition is unknown in *C. bivittata*; however, sperm displacement has been found thus far to be the rule in Coleoptera (Walker 1980). If sperm displacement does occur in *C. bivittata*, the last male to mate before oviposition would have the advantage in paternity. That last male advantage occurs in *C. bivittata* is suggested by the fact that copulation immediately precedes oviposition, and that when the female ceases to explore the trunk and drill, the male ceases to guard her.

I would argue, then, that small males of *C. bivittata* do not enjoy nearly as much reproductive success as their proportion of the copulations would suggest, and that there has not been intense selection for large males to assiduously expend energy excluding them from drilling females they are guarding. For small males, however, there must at times be an advantage to lingering near a female guarded by a larger rival, for otherwise one would predict that small males would avoid such females. If there is complete or partial sperm mixing in *C. bivittata*, there exists a possibility, however small, that a given copulation by any male at any time will result in fertilization. Even if sperm displacement is complete, there remains the possibility that the larger rival, distracted by competitors or a more attractive female, will not return before oviposition begins, leaving the way open for the small male to copulate last. Similarly, a small male that mates just after oviposition might still fertilize the next

egg to ripen if by chance the female went unmated during her next drilling.

The above arguments do not provide an ultimate explanation for why small males of *C. bivittata* enjoy greater mating success than small males of *B. anchorago*. Comparative studies are planned for these two species, which have similar breeding ecologies. Sperm competition and methods of detecting rivals will be explored, and the behavior and reproductive input of small, medium, and large males of both species will be compared. Possibly the system in *C. bivittata* represents an early stage of the development of dual male strategies, and may be a step on the evolutionary road to male dimorphism (Eberhard 1980). If so, elucidation of the differences between *C. bivittata* and *B. anchorago* could help our understanding of the selective environments favoring dimorphic male behavior and structure.

SUMMARY

Adults of *Claeoderes bivittata* aggregated on a *Quararibea* tree in Panama. Males ranging in length from 11–39 mm guarded and mated with females 12–29 mm long as they bored holes in the wood for their eggs. Fights often ensued as females tried to pry other females from their drilling sites; larger females more often won. Males fought males for access to females; larger males won significantly more often. Disputes involving males of similar size could be settled by a contest in which the two males stood closely parallel head-to-tail, while an antenna lashed a hind leg at either end. Such an appendage-lashing contest may permit rivals to assess one another's relative size.

Although individuals differing by at least 16 mm in length could couple, significant size-assortative mating was observed ($r = .4$). Due to the greater aggressive success of larger males and the fact that males rejected by females were smaller than males they accepted for mating, it was expected that mating males would be above average in size. Instead, mating males were significantly more likely to be large (≥ 31 mm) or small (≤ 22 mm). The disproportionate mating of small males may be explained in part by the tendency of smaller males to wait partly sheltered under a drilling female, emerging for copulation when larger males are not guarding the female.

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